POPULATION SIZE STRUCTURE OF *PARKINSONIA ACULEATA* ACROSS A RANGE OF HABITATS IN THE PALO VERDE MARSH

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Abstract.. The Palo Verde tree, *Parkinsonia aculeata*, dominates the seasonally flooded Palo Verde marsh. Current population size structure and distribution indicates that *P. aculeata* is unable to establish in areas heavily shaded by tree canopies or monospecific stands of cattail (*Typhia dominagensis*). It may also require an unusually long dry season to establish in regions of the marsh that are under water throughout most of the year, but it can tolerate and compete well in dry heavily grazed areas. Because of its apparent shade intolerance and its resistance to grazing, *P. aculeata* may actually increase in abundance in areas disturbed by humans and cattle.

INTRODUCTION

The Palo Verde tree, *Parkinsonia aculeata* (Caesalpiniaceae), occurs in high abundance in broad areas of the Palo Verde marsh, a 1200 ha marsh flooded by the Rio Tempisque in northwestern Costa Rica. At Palo Verde, *P. aculeata*'s range extends from the center of the marsh, where there is standing water cover for most of the year, to the dry outskirts of the marsh, where only periodic flooding occurs during unusually heavy rainy seasons. Despite its apparent ability to establish and grow in both dry areas and flooded areas, little is known about its ecological requirements, or about factors determining its distribution and abundance. In this study, I focus on the effects of shading, water stress, flooding, and grazing on the distribution and abundance of *P. aculeata*. By examining *P. aculeata* population size structure in different habitats, limitations to its establishment and growth can be determined.

P. aculeata occurs throughout Mexico and the American southwest, typically growing in or around washes in arid and semi-arid land (OTS staff, pers. comm.). It is recognized by its green photosynthetic branches covered in long sharp thorns, and its long (10-30 cm) lanceolate leaves often lined on both sides with small (approximately 5 mm in length) leaflets. In the drier areas of its range, it competes with five other woody species and non-woody herbs and cacti. In the marsh at Palo Verde, *P. aculeata* seedlings must compete with cattails and other littoral vegetation.

METHODS

Site description and disturbance history.

The Palo Verde marsh extends over a 1200-ha area from the Rio Tempisque towards the limestone hills and dry tropical forest to the north. The marsh is seasonal, and dries out completely during the last two months of the six month dry season which lasts from December to May (K. Stoner, pers. comm.). The wet season rains (mean annual rainfall 100-150 cm; Hartshorn 1983) typically refill the swamp in May or June, and late wet season rains often cause flooding to the edge of the surrounding forest. The soils of the marsh area are a mixture of fine particles from the surrounding limestone topography and volcanic material from the Rio Tempisque flooding (D. Peart, pers. comm.).

Cattle grazing began in the area in the 1920's and continued until it was banned in 1981. The marsh was characterized by large tracts of open water or areas dominated by *Nymphaea* spp. (Martin 1992) until 1981, when the marsh began to be invaded by cattails. Because marshes are rare in Costa Rica and are essential habitat for waterfowl, an effort to control cattail dominance was initiated in 1989. Areas of the marsh adjacent to the west end of the biological station's runway were cut and burned or cut, burned, and raked, and cattle grazing was reintroduced throughout the marsh (Jackson 1989).

Sampling.

Sampling was conducted between 12-15 January 1995, at the beginning of the dry season. A random north-south transect was located along the path east of the biological station's air strip. Five 10 x 10 m plots, spaced 20m apart, were sampled along this transect from the edge of the marsh standing water to the limit of *P. aculeata*'s range. An additional dry-land plot was selected randomly in a 50 x 50 m area to the east of the first transect, with a mature *Pithecellobium dulce* overstory. Four marsh plots (also 10 x 10 m) were selected randomly in a stand of *P. aculeata* bordered to the east by shallow water dominated by cattails and to the west with deeper water and non-emergent vegetation. The cattails in the area had been cut, burned, and raked in 1989.

In each plot, all woody plants were recorded and categorized in one of seven size classes. Seedlings and saplings were classed according to four height classes: small seedlings (<0.5 m), large seedlings (<1 m), small saplings (<2 m), large saplings (<3.5 m). Trees that had reached approximate canopy height (>3.5 m) were classed according to three diameter classes: small canopy trees (<7 cm), mature canopy trees (7-14 cm), and old canopy trees (>14 cm). In addition, woody species were categorized as tree species or shrubs based on whether individuals of near canopy height (>3.5 m) were present in the sampling area.

In all non-marsh plots, percent ground cover and canopy cover was assessed for the entire plot using six general categories: <10%, <25%, <50%, <75%, <90%, >90%. In all marsh plots, maximum and minimum water depth in the plot was recorded. In addition, water depth at base of tree was measured for each *P. aculeata* individual within the plots. In all plots, grazing damage to vegetation was noted, and quantified in terms of damage to leaf or stem tissue.

TABLE 1. Densities of *Parkinsonia aculeata* and other canopy tree species (individuals per $100m^2$ ±SE), % shading, and % ground cover in four habitat categories in the Palo Verde marsh area, Costa Rica.

	high-shade dry	medium - shade, dry	no-shade, marsh transition	marsh
	(n=1)	(n=3)	(n=2)	(n=4)
Density, *P. aculeata*	14	12.7 (±4.3)	3 (±0)	6 (±1.8)
Density, other tree spp.	6	4.3 (±3.3)	0	0
%canopy cover	75-90	25-75	0-5	25-50
% ground cover	50-75	50-75	5-50	NA

The plots were classified into four habitat categories based on amount of shading and water availability: (1) heavy shade, dry habitat (75-90% canopy cover); (2) medium shade, dry habitat (<75% canopy cover); (3) no shade (0-10% canopy cover), marsh transition zone (with moist, muddy soils or standing water ≤10 cm); and (4) marsh environment (standing water >10 cm throughout all areas of the plot).

RESULTS

The four habitat categories differed in tree densities, canopy cover, and ground cover (Table 1). The high-shade, dry habitat had a high canopy of *Pithecellobium dulce*, a lower canopy of *P. aculeata*, and a dense ground cover of herbaceous vegetation and woody shrubs, approximately 1 m in height. The medium-shade, dry habitat had a broken canopy of *Pithecellobium dulce* and *P. aculeata*, and a dense herbaceous ground cover intermediately disturbed by cattle grazing and trampling. The no-shade, marsh transition area had no canopy individuals, and a heavily grazed and trampled ground cover of grass and taller monocot marsh vegetation.

Size classes of *P. aculeata* were not evenly distributed across habitat

categories (Fig. 1). The high-shade, dry habitat plot had the largest number of canopy trees and had no individuals in the seedling or small sapling size class (individuals < 2 m tall). The medium-shade, dry habitat had individuals in all seven size classes, with a majority in the sapling and small canopy categories. *P. aculeata* individuals >3.5 m tall were completely absent from the two no-shade, marsh transition plots sampled. The four marsh plots had no seedlings present, and a relatively even distribution across three intermediate size classes. Woody trees other than *P. aculeata* were completely absent from both the marsh and the marsh transition habitats (Fig. 1).

In the four marsh plots, the size class distribution of *P. aculeata* appeared to be influenced by water depth (Fig. 2). Areas in shallower water had a more even distribution of individuals across the size classes. Deeper areas had a size class distribution dominated by mature canopy individuals. Deeper areas were better represented in the four plots (min. to max. water depths in the four plots were 10-23 cm, 26-50 cm, 37-54 cm, and 37-55 cm).

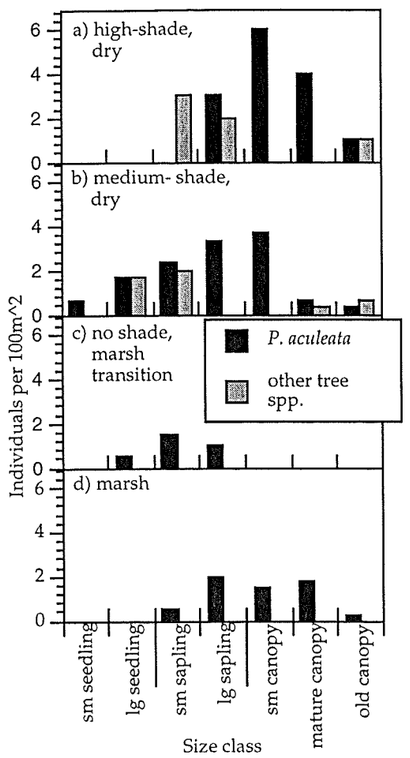

FIG. 1. Population size structure of *Parkinsonia aculeata* and other canopy trees spp. in four habitats in the Palo Verde marsh area, Costa Rica. a) high-shade, dry habitat: 75-90% shading, n=1. b) medium-shade, dry habitat: 25-75% shading, n=3. c) no shade, marsh transition: 0-5% shading, mud and standing water <10 cm, n=2. d)marsh: >10 cm standing water throughout plot, 25-50% shading, n=4. All replicates are random 10 x 10 m plots sampled on 13-15 January, 1995.

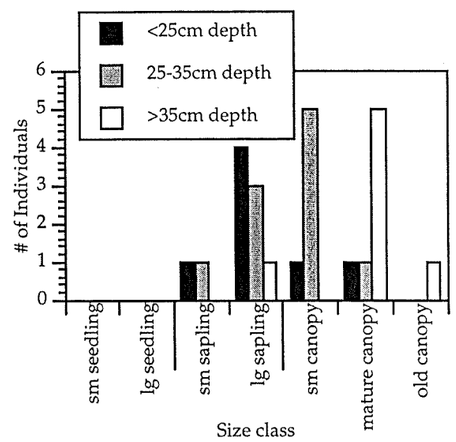

FIG. 2. Population size structure of *Parkinsonia aculeata* by water depth in the Palo Verde marsh. Depths measurements are based the water depth at base of tree on 14 January 1995.

Grazing was evident in all ten plots. The only evidence of grazing on *P. aculeata* was partial seedling leaf removal in the marsh transition habitat. All other woody species except *Acacia cornigera* had individuals with heavy grazing damage on leaves and stems. Qualitative observations indicate that grazing impact was lowest in the high-shade dry habitat, and highest in the marsh transition plots.

DISCUSSION

The absence of young *P. aculeata* individuals in the high-shade, dry habitat indicates that heavy shading may create unfavorable conditions for seedling establishment and growth. The presence ofyoung *P. aculeata* individuals in the higher light conditions of the medium-shade, dry habitat suggests that *P. aculeata* is capable of establishment and growth in the low moisture conditions of the dry habitat, but is limited under a more dense canopy. Thus *P. aculeata* appears to be highly shade intolerant.

Despite its specialization and dominance in the marsh area, dry conditions do not seem to limit the distribution of *P. aculeata*. The potential for water stress in the two dry habitats is indicated by the presence of plants typical of harsh dry conditions, such as the cactus *Lemaireocereus aragonii*. Yet the highest density of *P. aculeata* was found in the dry habitat plots, which suggests that it may grow better outside of the marsh environment, in the absence of competitors which would eventually out-shade *P. aculeata*.

Despite the abundance of light and absence of other woody competitors, *P. aculeata* exists in the lowest densities in the no-shade, marsh transition plots. This seems contradictory to the argument that it is limited by competition for light. However, it appears that the local area sampled in this study may be undergoing succession of *P. aculeata* after a recent disturbance. The presence of mature *P. aculeata* individuals in the marsh transition areas adjacent to this plot suggest that the area sampled is not representative of the marsh transition area as a whole. In addition, the heavy grazing and trampling may be a factor in the lower overall densities of *P. aculeata* in marsh transition habitat.

In the marsh area, the establishment of *P. aculeata* seedlings may be dependent on a rare, extended dry season, leaving barren land for a length of time sufficient for seedling establishment. Seedlings that begin growth near the end of a normal dry season would be inundated with water after the 2-3 month dry period ends and the standing water returns to wet season heights. It seems implausible that the seedlings can persist underwater, especially if the water surface is covered by a thick layer of floating vegetation. As relative water depth increases, the frequency of a sufficiently long dry period would decrease. I would, therefore, expect a more even distribution among the size classes in the shallower areas, where dry periods are presumably longer in duration. The finding of a size class distribution skewed toward domination of the oldest individuals in the deeper areas, as well as the overall absence of seedlings in the marsh plots supports this "rare, extended dry season" argument.

The abundance of *P. aculeata* may also be facilitated by human and cattle disturbance. The large area of the Palo Verde marsh dominated by monospecific cattail stands had a very low density of *P. aculeata*, and this population seemed composed entirely of mature and old canopy size class. It appears that *P. aculeata* seedlings may be unable to establish and grow in the dense cattail stands. Similarly, the shade intolerance of *P. aculeata* seems to prevent seedling establishment under a thick canopy. Thus where cattails dominate or a dense overstory is present, human or cattle disturbance may be required for *P. aculeata* recruitment. In addition, heavy cattle grazing in some areas of *P. aculeata*'s range (for example, the marsh transition habitat) may deter or prevent colonization by other woody competitors which lack the thorny defenses that make *P. aculeata* resistant to grazing.

Several aspects of *P. aculeata*'s life history and physiology deserve further study. Apparently, no knowledge exists about possible dispersal limitations, or the exact mechanism of dispersal. The fact that *P. aculeata* seed pods float, as well as the distributional patterns of *P. aculeata* which coincide with the range of area that is seasonally flooded, indicates that flood water may be the primary method of dispersal. It is also possible that seeds are dispersed by mammals or birds, which seem to actively forage on the seed pods of *P.*

aculeata. There is also no indication of what allows *P. aculeata* to thrive in both aquatic habitats and extreme dry areas with only periodic flood water. A study of the variation in root structure between underwater and dry area roots may yield some insight into how phenotypic change might allow growth in both extreme environments. Finally, further study of the population structure of this tree may be more instructive in the large expanses dominated by *P. aculeata* on the south side of the marsh, which does not have the same history of human disturbance.

Overall, *P. aculeata* appears to be highly tolerant of both water stress and grazing pressure. While its primary area of occurrence is within the marsh, it appears that seedling establishment may only occur in these areas during rare, extended dry seasons. Though *P. aculeata* appears competitive with other tree species in dry, open canopy areas outside the marsh, it may be both shade intolerant and incapable of growing to a height sufficient to avoid being overshaded by taller canopy trees. The combination of its shade intolerance and its resistance to grazing appears to make *P. aculeata* more competitive in areas of human disturbance to canopy trees or cattails and in areas of heavy cattle grazing.

LITERATURE CITED

Hartshorn, G. S. 1983. Plants: Introduction. in Costa Rican Natural History. D. H. Janzen., editor, University of Chicago Press. p118-157.

Jackson, P. 1989. Percent plant cover and richness according to different management treatments at the Palo Verde marsh. OTS Tropical Biology 89- 3:208-215.

Martin, K. 1992. Estimation of animal diversity and abundance in the Palo Verde marsh habitats. OTS Tropical Diversity 92:45-48.